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Justice and fairness related behaviors in non-human primates

Sarah F. Brosnan

Abstract

A distinctive feature across human societies is our interest in justice and fairness. People will sometimes invest in extremely costly behavior in order to achieve fair outcomes for themselves and others. Why do people care so much about justice? One way to address this is comparatively, exploring behaviors related to justice and fairness in other species. In this paper, I review work exploring responses to inequity, prosocial behavior, and other relevant behaviors in non-human primates in an effort to understand both the potential evolutionary function of these behaviors and the social and ecological reasons for the individual differences in behavior. I also consider how these behaviors relate to human behavior, particularly in the case of experimental studies using games derived from experimental economics to compare non-human primates' responses to those of humans in similar experimental conditions. These results emphasize the importance of a comparative approach in order to better understand the function and diversity of human behavior.

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1. Introduction

A feature of humans that apparently sets us apart as a species is our focus on others' well-being as well as our own (1-3). We will, sometimes at great personal cost, protest outcomes that we consider unfair, whether they personally affect us or have no direct impact on our lives. What is it that causes people to behave in this way? One possibility is that it is due to culture. In fact, only English has a word for the concept of "fairness"; other languages have adopted the English word, indicating a culturally broad interest in the concept, but potentially implying that the concept is not ubiquitous (4). Another possibility is that we have evolved to be interested in the well-being of others. While there are clear fitness benefits to considering one's own well-being, there are also (more delayed) benefits to considering others' well-being. There may be costs to helping others in the short term, but if there are long-term benefits, either due to continued interactions based on reciprocity or, more indirectly, due to gaining a reputation as a "fair" person, then the behavior can be selected (5). If this behavior has evolved, we may find similar behaviors, or precursor behaviors, in other species. Other species will not show these behaviors in the same way that humans do. Among other reasons for this, many behaviors related to fairness and justice, such as the ability to share information about a third party's previous behavior, require language. Nonetheless, an important question is the degree to which fairness and justice have evolved from similar sorts of behaviors in other species. This evolutionary approach provides insight into understanding our own behavior.

In humans, the concept of fairness is closely related to that of justice. Distinguishing the two, fairness involves voluntary interactions with other individuals, while justice is meted out by an impartial third party (4). Based on these definitions, most of the experimental work discussed below relates to fairness, rather than justice, as the subjects being studied are involved in the interactions and outcomes in question. Outside of the experimental context, observations suggest impartial interventions in others' interactions, indicating that these species may also be sensitive to justice concerns. There are many different aspects of justice and fairness, including distributive, procedural, retributive, restorative, etc. Most experimental studies involving non-human species measure subjects' responses to different distributions of food rewards, and hence concern distributive justice or fairness. In humans, two common distribution mechanisms are egalitarianism, in which all individuals get the same outcome (e.g., equality) and equity, in which individuals' benefits are proportional to their inputs. Both of these are amenable to study in other species, and are the feature most commonly manipulated in the aforementioned experimental studies (e.g., by altering subjects' payoffs as compared to their partner's). Outside of the experimental realm, observational studies indicate that non-human primates are also sensitive to non-distributional aspects of justice and fairness, such as judging the appropriateness of another's behavior, providing a broader context in which to consider justice or fairness in these species.

Studying other species' behaviors in these situations allows us to elucidate the evolutionary function of justice and fairness by exploring behaviors that are related, either because the behavior itself is a component of justice or fairness, or because it represents a precursor to human behavior. Studying other species is informative in two complementary ways, through homology and convergence. Homologies occur when a behavior exists in multiple species because the behavior existed in a shared common ancestor. This pinpoints when in the taxon's phylogenetic history the trait evolved. Convergences occur when a behavior evolved in multiple species due to common selective pressures, but without shared descent from a common ancestor. Convergences may be particularly informative when studying the function of a behavior as, through comparison across species, they may indicate which traits co-occur and the social or ecological pressures that may have selected for the behavior.

My goal in this review is to bring together data regarding behaviors related to justice and fairness in non-human primate species (hereafter, primates). Observations have highlighted situations in which primates act as if their behavior is guided by an interest in the outcomes of others (6, 7). A decade ago, the first experimental studies emerged, focusing on one aspect of justice and fairness: how individuals responded to getting less than a partner (8, 9). These studies utilized methods derived from game theory and showed that, in experimental settings in which inequity between two individuals was introduced, subjects responded negatively to inequity not in their favor. Since that time, this task has been extended to

fourteen species, including ten primate species, allowing for a broad phylogenetic view that provides insight into the evolutionary function of inequity (10). Additionally, responses to inequity have been explored in more species-specific contexts and situations (11, 12). These results highlight the correlation between inequity and cooperation as well as emphasizing the socio-ecological factors that influenced the emergence of justice- and fairness-related behavior. This comparative analysis is beginning to shed light on the factors that may have led to the evolution of justice- and fairness-related behaviors in humans and other primates (13).

2. Justice and fairness related behavior in other species

One hypothesis for the evolution of fairness is that recognizing inequities helped individuals ascertain the value of their partners in cooperative interactions (10, 14). Individuals should not continue to work with others if they do not, on average, benefit from the relationship. Whether outcomes are equitable may be used as a proxy; if one's outcomes are routinely wanting as compared to one's partner's, then it is likely that an interaction with another partner, even one chosen at random, will lead to a more beneficial outcome. This leads to a partner choice mechanism in which individuals sample other partners when they are experiencing high levels of inequity with the current partner or partners (15). Note that individuals thus recognize and respond to inequity without any understanding of why they are doing so. Additionally, this provides a benefit even if the individual's outcomes in the less advantageous interaction are net positive, as the currency of natural selection is relative, rather than absolute, gains.

While this hypothesis linking inequity and cooperation emerged in the context of humans, other species also cooperate with one another, so behaviors related to inequity may occur in other cooperative species as well. Comparative research is challenging. First, the manifestations of justice and fairness may be different in different species, making it difficult for human experimenters to recognize relevant behaviors. Second, non-human species are non-verbal, with the dual implications that we cannot ask them about their motivations for their behavior, nor can we ask them about outcomes that did not result in an overt change in their behavior. Thus, we will miss any response that does not have a behavioral manifestation. As a result, experiments focus on whether other species act in a certain way, not whether they *mean* to act in that way. Finally, the limitation to measuring behavioral changes means that the methods utilized in humans typically differ substantially from those used in other primates, which can complicate comparative analyses.

There have been two approaches to comparative work on justice and fairness. The first is to adapt game theory methods to explore decision-making in other species. Game theory is a powerful approach that allows complex decision making to be modeled experimentally as a series of carefully controlled choices, which can be experimentally manipulated to rigorously explore the behavior of interest (16). The advantage of game theory for comparative research is

the focus on very simple choices to uncover complex behavior, making these techniques amenable to use in a wide variety of other species. Procedures can be designed that require no verbal instruction whatsoever and that can be used in the same form in humans and other species, allowing for direct comparisons and subsequent explorations of shared outcomes or cognitive mechanisms (17). While we cannot assume that different species (or different individuals within the same species) interpret identical procedures in the same way, if procedures differ between species then we are never able to disentangle whether any resulting differences in behavior are due to species differences or differences in the procedure. One challenge to experimental approaches is that humans interact with an experimenter of the same species, while other species interact with an experimenter of a different species (a human). While this is a practical necessity, other species did not evolve to interact with humans, and so careful controls are needed to determine that the non-human subjects were evaluating their outcomes relative to their conspecific partner, not the experimenter. Additionally, experimental approaches are artificial, and so we may miss situations in which justice-related behavior occurs. Despite these drawbacks, game theoretic approaches have the advantage of being comparable to the human literature and so are indispensable for comparative research.

A second approach is to explore behaviors that may be related to justice and fairness in species-specific contexts. This includes observational studies, in which behavior is observed during unconstrained interactions. This approach has the advantage of being the most natural, which leads to likely candidate behaviors and a better understanding of how justice or fairness manifest in the species' typical interactions. Moreover, as these studies are not reliant on manipulating outcomes and measuring subjects' subsequent behavior, there is the opportunity to study justice outside of the context of food distributions. The disadvantages are that these results are less comparable across species, particularly if methods or the contexts in which individuals are attentive to inequity differ, and the underlying motivations for subjects' behavior are not known. The ideal is to combine insights from both approaches.

3. Using game theory to explore justice-related behavior

3.1 The Ultimatum Game

In 1982, Werner Guth presented the Ultimatum Game (UG), designed to explore fairness in bargaining behavior in humans (18; see Figure 1). In this game, one individual, a proposer, is given a set sum and told to allocate it between him or herself and a partner. If the partner, called the responder, accepts the allocation, both parties receive the money as allocated, but if the responder rejects it, neither party receives anything. Hundreds of experiments across the last three decades have shown that modern Western humans typically allocate about 40% of the sum to the responder, and responders typically reject anything under about 20% of the allocation (19). Allocations are higher than those seen in a related game, the

Dictator Game (DG; Figure 2), in which the responder has no recourse to the proposer's allocation, indicating that the proposer alters his or her allocations dependent upon whether the responder can influence the outcome.

The UG is often considered to measure fairness preferences, thus it is particularly relevant to considerations of fairness and justice in other species. There have been two studies in chimpanzees, both relying on a limited-form version of the game, in which proposers make a choice from between two pre-set distributions (Figure 3). In neither case did chimpanzee responders refuse allocations, however proposers' behavior differed between the studies. In the first, proposers chose between the two trays, each of which contained foods for them and their partner (neither chimpanzee could reach their partner's food). After the proposer chose one option, by pulling the corresponding tray within reach of the responder, the responder could choose whether or not to accept the offer by pulling the tray in such a way that both the proposer and the responder could access their rewards. In this study, proposers consistently chose the larger outcome for themselves and responders accepted virtually any offer (20). However, responders accepted more than half of zero offers (e.g., they received nothing themselves), indicating that they may not have understood the task. A subsequent study showed that human responders rarely refused in a similar situation (21), indicating that the deviation from behavior typically seen in the UG could have been due to the experimental design.

In a more recent study (22), subjects were trained that one token represented an equal 3/3 split of six food items while the other represented a 5/1 split of the foods in favor of the proposer. Proposers could choose a token and pass it to the responder, who could then trade it out to the experimenter (accepting the proposal) or not (refusing it). Proposers' choices in the UG were compared to those in a DG-like condition in which the responder was present, but had no recourse (proposers passed the chosen token directly to the experimenter). The procedure was repeated using children paired with another familiar individual from their daycare class to ensure that humans would respond similarly to chimpanzees in this procedure.

Despite responders never refusing offers, all chimpanzee proposers' choices shifted from preferring the more beneficial 5/1 token in the DG-like condition to preferring the equal 3/3 split in the UG. Validating the procedure, children responded in the same way. These results differ from typical UG results because neither the children nor the chimpanzees ever refused the low offer. However, in typical human UGs, responders are interacting with anonymous partners, and their only recourse is to refuse the offer. In this study, responders were interacting with individuals from their social group and had options besides refusal, such as punishment or the threat of punishment, which are less costly means of protest than refusing a positive, if relatively smaller, outcome (23). Similarly, in typical UGs, proposers' refusals decrease when they are given other options (e.g., the responder can write a note to the proposer; 24). These results do not necessarily mean that the chimpanzees showed a sense of

fairness, as if this were this the case, they should have preferred the equal token in both the DG and the UG conditions. This also does not mean that proposers had prosocial motivations, as they may have changed their preference to avoid refusals by the responder. Nonetheless, both humans and chimpanzees were apparently sensitive to how their choices influenced their partner's decisions, and changed their behavior accordingly.

3.2 The Impunity Game

Closely related to the UG is the Impunity Game (IG; Figure 4). The IG is similar to the UG, but if the responder refuses the proposer's offer, the responder gets nothing while the proposer receives their portion of the allocation as indicated by the proposer (25). This game has received very little attention in the human literature, in part due to the assumption that no rational responder would ever refuse an offer, as this action leaves them with both absolutely and relatively less than the proposer (in the UG, a refusal leaves the responder with absolutely less, but relatively the same as, the proposer). Nonetheless in a study that used the same procedure for both games, human subjects refused in the IG about half as often as in the UG for a given distribution (26).

Much as in the UG, the challenge of the IG with primates is assuring that the responders understand that their choice was constrained by the actions of the proposer. Most studies of primates to date have explored only responses to unequal distributions, to learn how individuals respond to inequity when they cannot alter their partner's outcomes (reviewed in 27). In a typical experiment, paired subjects alternate completing a task (such as exchanging a token) with a human experimenter. The experimenter rewards subjects with the same rewards (Equity condition) or gives one a more preferred reward (Inequity condition). To rule out the possibility of contrast effects (28, 29), in which subjects compare their outcomes to those present in the environment without attending to the social component, pairs are given a Contrast condition in which both partners are shown the preferred reward but, after completing the task, receive the less preferred one (30, 31). These responses are referred to as Inequity and Equity rather than Inequality and Equality because, despite the fact that the outcomes are identical (or not), we cannot know if they are perceived identically by subjects due to differences in rank, hunger level, etc.

Initial studies confirmed that both capuchin monkeys (8, 32, 33) and chimpanzees (9, 31) were more likely to refuse to complete the interaction (e.g., return the token or accept the subsequent food reward) in the Inequity condition as compared to either the Equity condition or the Contrast condition, although there was variation within and between studies (discussed below in more detail; 9, 34, 35). Since humans refuse more frequently in situations in which they do not like the outcome (e.g., in the UG game), this similar behavior in other species has been interpreted as responding negatively to inequitable outcomes. The response is also sensitive to context, with refusals occurring only after subjects have completed a task, but not

when rewards are simply handed out for "free" (29, 35-38). Despite this, subjects do not change their rate of refusal when they have to work harder than a partner to achieve their reward (39, but see 40 for an exception). This indicates that while subjects are sensitive to inequity in the context of joint action, it is the difference in outcome rather than effort that is important for their decision-making. This may indicate that subjects are more sensitive to distributional inequities than procedural ones.

Demographic variables also influence individuals' responses, but not always in consistent ways. For instance, not all studies show a dominance effect, although for those that do, dominant individuals always respond more strongly than do subordinates, presumably because they are more accustomed to receiving higher-valued rewards (31, 34). There are also no consistent sex differences (9, 31), possibly due to relatively small sample sizes (although several dozen chimpanzees have been tested across three facilities, a large sample for captive primate studies, this is a very small sample size for untangling individual variation). The degree to which individual differences influence behavior – both in non-human and human primates – is a topic that requires additional exploration.

Finally, not all primate species refuse in conditions of inequity. The same procedure to elicit inequity has now been used to test seven primate species, and similar procedures have been used with several others (see Table 1). Comparing these different species' responses allows us to consider which social or environmental factors may have played a role in shaping the evolution of the response. While more species will need to be tested to verify these conclusions, patterns are emerging. For instance, responding negatively to inequity is not a homology within the primates. Among the great apes, bonobos may respond similarly to chimpanzees and humans, indicating that the last common ancestor of *Pan* and *Homo* shared this behavior. Only five bonobos have been tested, making statistical analyses difficult, however their refusal rates doubled from 10% to 20% in the Inequity as compared to the Equity condition (34). On the other hand, orangutans showed no response to inequity (34, 41), eliminating the possibility of a homology within the great apes. Additionally, the behavior is not a homology within the New World monkeys, as of the five New World monkeys tested, only capuchins responded differently to the inequity condition. The orangutan's behavior also rules out the possibility that this is related to increased brain size or advanced cognitive capabilities, as orangutans have a similar brain-to-body ratio and cognitive skills as the other great apes.

Thus far, negative responding to inequity correlates positively with whether a species cooperates routinely with non-kin (reviewed in 10; see Figure 5). Chimpanzees, bonobos and capuchin monkeys cooperate with non-kin, for instance in coalitions and alliances, and all three species responded to inequity in these experiments. Macaques, too, both responded negatively to inequity (42, 43) and show cooperation in the form of coalitions and alliances (44). However in squirrel monkeys, a species confamilial (and sympatric) with capuchins, but lacking extensive social cooperation, males responded more strongly to the Contrast condition than either the

Inequity or Equity conditions, indicating that their reactions were more strongly influenced by their previous offers than by those received by another monkey (30). Again considering orangutans, one way in which they differ from chimpanzees and bonobos is their relative lack of social cooperation. A potential difficulty arises with the species that show bi-parental care. These species cooperate extensively, working together to raise offspring, but none of the species tested in this paradigm thus far have shown evidence of responding to inequity (37, 45). However the proposed function of responding to inequity is to judge the value of cooperative partners in order to determine whether to search for a new partner. It is very costly to find a new pair mate, so it is possible that even if individuals in bi-parental care species do notice inequities, they have evolved to respond only to large inequities, which does not include receiving a less preferred reward than their mated partner.

Related to this, subjects should be more sensitive to inequity when forming a relationship, which is a time when the costs of finding a new partner are less, than after the relationship is established and there is joint investment in offspring (10). One drawback to our understanding of human behavior is that most studies to date have involved unrelated individuals, mostly strangers, virtually always in conditions of anonymity, and often without repeated interactions, which removes the possibility of reputations forming. While these conditions are informative for exploring the degree to which humans will cooperate without either a relationship or social knowledge, this is not as informative for telling us about typical human cooperative behaviors, which primarily take place within established relationships with known partners. Additional experiments that explore differences in behavior in the context of different social relationships and with different degrees of anonymity will be essential to understand how inequity functions in the context of the relationship.

3.3 Prosocial Games

Despite children's calls of "that's not fair" when they receive a less preferred outcome than another child, responding negatively to receiving less than one's partner is only one part of a sense of fairness. A sense of fairness or justice requires responding not only to inequities that affect oneself, but also to those that affect others (14, 46, 47). This has been explored most commonly using procedures reminiscent of the Dictator Game. In the typical experimental game with primates, the subject has the option to provide rewards, or not, to a social partner. Importantly, the subject's behavior with a social partner is compared to their behavior when alone, ruling out the possibility that they are choosing the prosocial option because there are a greater number of rewards visible than in the non-prosocial option. The critical difference between these games and the DG is that choosing to reward the partner does not reduce the subject's own payoffs in these prosocial games, thus there are no disincentives for prosocial behavior.

Although reward structures have varied across experiments, making direct comparisons difficult, a sufficient number of these studies exist that patterns are emerging. Chimpanzees choose to bring rewards to their partners in some experiments (48), but not others (49, 50), and it is not yet clear which features lead to prosocial behavior in this ape. It is also not clear that these results are reflective of chimpanzees' prosocial tendencies. Results in the inequity studies described above imply that chimpanzees may recognize when they receive a better outcome than a partner even when they chose not to act to change the situation. In these studies, subjects sometimes refused preferred rewards when their partners got less preferred ones, and did so at greater rates than when both received preferred rewards (31). This does not mean that the subject's motivations were prosocial, as they may have feared the partner's reaction to receiving a less preferred reward than the subject, but these results verify that chimpanzees recognized when they received better outcomes than a partner.

Among the monkeys, capuchin monkeys preferentially chose the prosocial option (51, 52), and were more likely to reward kin than either non-kin group mates or non-group mates (51). Callithrichids, one of the taxa that show bi-parental care, also chose the prosocial option that rewarded a group mate (53, 54), although like the chimpanzees, they did not do so in all experiments (55, 56). Finally, long-tailed macaques also showed prosocial behavior, but in this study dominants chose the prosocial option while subordinates did not (57). Again, these studies measured behavior, not motivations, so they cannot shed light on why the monkeys behaved prosocially (e.g., they cannot disentangle whether subjects were prosocially motivated to help their partners or were selfishly motivated to avoid repercussions for not helping their partners). Nonetheless, while there is still debate about the contexts under which each of these species show prosocial behavior and the selective pressures underpinning it, in some circumstances all of the primates tested thus far actively chose an outcome that benefitted a partner as well as themselves.

4. Species specific approaches to justice and fairness

4.1. Inequity in the context of cooperation

If responding to inequity is a mechanism for identifying good cooperative partners, then inequity should influence behavior when cooperation is required. This can be experimentally explored by introducing inequity into an experimental cooperation paradigm. Capuchin monkeys have been studied extensively in the realm of cooperation and there is evidence that they understand the contingencies of cooperative tasks and are sensitive to their partner's behavior (reviewed in 58). In the first study to explore cooperation in a situation of inequity, capuchin monkeys could work together to pull in a heavy tray to obtain food, but only one monkey got the food. Monkeys worked together, but only if the individual who received the food shared with the individual who did not. Perhaps anticipating this, the monkey who got the food was more likely to share in this condition than in a control condition in which they could

acquire the food without their partner's help. This indicates a sensitivity to their partner's reaction and an anticipation of their need for their partner's help (12).

In a study more explicitly exploring inequity and cooperation, monkeys were tested in a similar paradigm in which both monkeys always received food, but these foods differed in the degree to which the monkeys preferred them. Thus, sometimes both monkeys received the (same) preferred food, sometimes they received the (same) less preferred food, and sometimes one received the preferred food while the other received the less preferred food. The monkeys were not separated nor were their roles pre-determined by the experimenter, so in all cases, the monkeys had to negotiate between themselves who would pull from which location, which also determined who got which food item. The pair's pulling success was not dependent upon the value of the rewards; pairs pulled in the tray just as often for two identical rewards as for two different ones. Instead, the monkeys were sensitive to their partner's behavior. In some partnerships, individuals shared access to the more preferred reward when the rewards differed, each receiving it approximately half of the time. In these partnerships, cooperative pulling success was high (approximately 70%) in all three conditions. On the other hand, for partnerships in which one member dominated the preferred reward in the different-reward condition, they succeeded in pulling in the tray only about 30% of the time across all three conditions (11).

. These results show two important things. First, subjects in the inequitable partnerships apparently reacted against their partner, not the reward distribution. That is, when one member dominated the preferred reward in the different-reward condition, pulling rates dropped across all conditions, even the two conditions in which both monkeys got the same reward. This supports the hypothesis that recognizing inequity helps to identify cooperative partnerships, as these subjects refused to work with a specific partner rather than refusing a certain outcome. Second, in the partnerships in which neither individual dominated the preferred rewards, subjects were, by definition, receiving the less preferred reward on half of all different-reward trials, yet cooperation was maintained. The reality of cooperation is that it is unlikely that every individual will receive the same reward on every trial, and these results indicate that capuchins are somehow able to extrapolate across multiple trials and therefore reap the gains of cooperation despite variation in outcome.

4.2 Inequity in interactions with the experimenter

While the above data relate to primates' rewards in comparison with each other, how do primates react towards the experimenter who caused the inequity? A recent study explored which of two novel experimenters the monkeys preferred to interact with in a task in which the monkey returned a token to an experimenter in order to get a food reward. Subjects first gained experience with both experimenters, one of whom consistently provided the offered rewards and one of whom failed to provide the offered reward (or any reward) on up to 50% of

trials. When the monkeys then had free choice as to which experimenter they would return the token to, subjects were equally likely to interact with both experimenters (59). While it may be that capuchin monkeys do not form preferences for experimenters based on reliability (they do show preferences between experimenters in other situations; 60), it is also possible that the relationship between humans and captive non-human primates influenced the results. Despite the fact that subjects in (59) had never interacted with the experimenters who participated in the study, they did have extensive experience with experimenters in general, as well as with trials in which rewards were not given (e.g., because of incorrect responses). Thus they may have responded to this situation by trying to "correct" their response rather than recognizing the experimenter's unreliability. Pet dogs, who may have a different relationship with humans, do discriminate between human experimenters in a similar task (61).

4.3 Inequity in social interactions

Some of the best evidence in favor of a sense of justice or a sense of fairness comes from observational studies of non-human primates' interactions during their natural behavior. These interactions also offer the opportunity to look beyond distributional equity. Unfortunately in many cases these events are extremely rare, making it difficult to make strong statements about these behaviors. Moreover, observational work yields correlations, which cannot tell us causation without controlled studies that alter one variable at a time. Nonetheless, these situations may be the best window we have into primates' sense of fairness and justice as they are natural interactions, unconstrained by human behavior or experimental contingencies.

Chimpanzees display a sense of "social regularity" that has been linked to the human sense of justice (6). Chimpanzees appear to have expectations about others' behavior, and are known to express frustration, sometimes aggressively, when these expectations are violated. Moreover, such responses are not limited to the apes. Apes and monkeys both engage in policing behavior in which individuals, typically the highest-ranking males, intervene in fights to maintain group stability. Some of the best evidence for the utility of policing behavior comes from studies done with macaques. In these studies, the groups' behavior was compared on typical days and those in which the highest ranking males were removed. Results demonstrated the males' necessity in stabilizing the group's interactions (62, 63). Similarly, both macaque and chimpanzee males, once they have established high status, will intervene in fights on the side of the loser (64, 65). While there are many reasons for such behavior, it again indicates that these males recognized social inequalities in others' interactions and were willing to act against their own short-term self interest to rectify them. Of course, in the longer term, maintaining group stability always benefits a high-ranking male, and a physical intervention may additionally emphasize his power to others in his group. Nonetheless, there are short term costs to entering into any fight, particularly in favor of an individual who is losing.

Recently, inequity has also been linked with play fighting in gorillas. Gorillas who gained the upper hand during a bout of play fighting worked to maintain it, possibly indicating that they were aware of the social dynamics and strove to maintain their competitive advantage (66). The authors emphasized the benefit of studying inequity in a natural social context, and considered how responses to inequities may vary depending on whether the individual in question has the social advantage. Again, for practical experimental reasons, much work focuses on inequity of food rewards, but attention to inequity may have evolved in the social realm, and only more recently adapted to physical outcomes, such as food. Future work will help to determine how responses to inequity vary depending upon the commodity in question.

5. Inequity and related behaviors

Inequity likely interacts with other behaviors, although thus far there have been few studies to explore these interactions. Below I briefly consider a few potential areas of interest.

5.1 Punishment

Recognizing inequity is only one of several behaviors that likely underpin cooperation. Punishment may also support cooperation. Cleaner fish, who cooperate with non-kin during the cleaning interaction, do not respond to inequity of rewards as compared to a social partner (67). However, the fish do punish one another for acting against the pair's interests (68). Thus, it may be that in species or situations in which finding a new partner would be difficult or costly, punishment to change the current partner's behavior is used in lieu of finding a new partner (69).

5.2 Inequity and contrast effects

It seems likely that responses to inequity share cognitive mechanisms with behaviors such as loss aversion and contrast effects, both of which involve reactions to unexpectedly lesser outcomes. These are rather difficult to untangle experimentally given that inequity is essentially a contrast effect with the others' outcome as the referent (similarly inequity is a loss with the other's outcome as the referent). However, we can compare the relative strengths of these motivations using well-designed experiments. For instance, while some species (e.g. chimpanzees and capuchin monkeys) were more sensitive to inequity with one's partner than to contrast with previously offered outcomes, others (e.g. squirrel monkeys) showed the reverse. Mapping such preferences may help to determine the underlying influences on the expression of these behaviors, providing insight into the relative strength of social and non-social environmental stimuli on a species' decision making.

5.3 Inequity and delay of gratification

In order for an animal to refuse a reward as a means of displaying displeasure, they must be able to delay gratification (70). Turning down an immediate food reward is not something that most individuals will easily do, even for a potentially greater payoff in the future. However, if the hypothesis that individuals' tendency to do so is related to cooperation is correct, then a negative response to inequity may involve expectations about what an individual will, should, or could receive in the near future. This is similar to delay of gratification, albeit with a far less certain future outcome, suggesting that the act of refusing may be scaffolded by the individual's ability to delay gratification. Of course, the animals need not understand this logic, but this may be an underlying mechanism of responding to inequity, or a frequent need to respond to inequity may provide selective pressure to improve a species' ability to delay gratification. Supporting this link, several primate species that respond negatively to inequity are able to delay gratification for comparatively long periods of time (71-73). It will be interesting to see how this and other cognitive mechanisms influence individuals' ability to respond to inequity.

6. Future Directions and Conclusions

Although in the previous decade we have learned much about non-human primates' responses to inequity, there remains much to learn. First and foremost, humans are primates, which makes non-human primates a natural group for comparison, yet other species also respond to inequity (61, 67, 74, 75). More work is needed to identify which species respond to inequity, whether these responses are similar across species, and the nature of individual differences in response in these species. This will also provide a stronger test of the hypothesis that inequity responses correlate with cooperation.

Another important area of inquiry is distinguishing situations in which non-human species notice versus respond to inequity. All of the studies described above focus on behavioral responses to differing outcomes, but subjects may notice an inequitable situation that they do not to respond to, for instance because they are unable to inhibit their desire for the reward, because of social pressure, or for other reasons not yet known. One way to address this question is to explore changes in individual's affect across different conditions to identify responses that occur in the absence of a behavioral response. This approach has been successful in identifying recognition of inequity in young children (76).

Inequity also occurs in a variety of contexts that are not yet reflected in the non-human literature due to the focus on distributional concerns in experimental tests. One major focus of human research that has received little attention in the non-human literature is procedural inequity (77). Although preliminary investigations reveal no change in subjects' behavior based on procedural variations (31), non-human primates have expectations about others' behaviors and it is reasonable to assume that they are sensitive to procedural differences.

One limitation of the existing experimental research related to justice and fairness is that it typically involves interactions between non-human primates and human experimenters. Although the comparisons that the primates make are typically with a conspecific, the experimenter mediates the interaction and determines the rewards. It is possible to design experiments that largely remove the human presence (e.g., 11), and future work in this direction would be informative.

All of the experimental work to date has involved an egocentric approach to fairness and justice, yet observational studies of natural behavior indicate that primates will intervene in the interactions of others, in some cases impartially. Although challenging, it is possible to study fairness in the lab removed from egocentric reactions. Experimental studies on reputation in chimpanzees indicates that these apes are able to form opinions about human experimenters from watching these experimenters interact with other chimpanzees (78, 79). A fruitful line of inquiry would be to explore non-human primates' judgments of the equity of others' interactions. Such third-party assessments of others' distributions would be the first research to experimentally examine justice in other species.

Finally, studies of justice and fairness will advance significantly when work from the lab is combined with what we know about animals' natural behaviors in the wild (80). In this way we will better understand the social and ecological conditions under which these preferences manifest, which lends additional insight into their function.

Humans are not alone in responding negatively to differential treatment as compared to a partner. This response is shared with other species, and appears to be instrumental in successful cooperation. Understanding the evolution of this response provides insight into our own behavior. While non-human primates do not show a sense of justice or fairness in the same way as humans do, gaining knowledge about the evolution of justice and fairness from comparative studies will improve our understanding of these judgments in humans as well.

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Figure captions

Figure 1: A schematic diagram of the Ultimatum Game (UG).

Figure 2: A schematic diagram of the Dictator Game (DG).

Figure 3: A schematic diagram of the limited form UG; in this version, the proposer can choose between two options.

Figure 4: A schematic of the Impunity Game (IG). The full IG has not yet been explored with other species, however a typical inequity procedure is reminiscent of the Responder's choice in the IG (indicated by the dotted line). That is, the Responder must choose whether or not to accept a distribution, but their choice does not influence their partner's outcome (in the typical experiment, the human experimenter functions as the Proposer, so the Responder's partner is not responsible for the outcomes).

Figure 5: A schematic diagram indicating the responses to inequity of subjects that have been tested using the typical inequity procedure in which subjects exchange tokens for rewards while sitting next to a partner. Note that this diagram excludes gorillas, for whom too little information is known. Photo of the macaque and bonobo by F.B.M. de Waal, photo of the

orangutan by C. Talbot, photo of Darwin from the public domain, and all other photos by the author.